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Early outflying and late homeflying in the Indian pygmy bat under natural conditions

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Abstract. The outflying and homeflying activity pattern of a colony of the Indian pygmy bat *Pipistrellus mimus* occupying a tunnel was studied under natural conditions. Before leaving the tunnel for foraging, the bats made circling flights outside to sample the environmental light conditions. The onset and end of activity was related to the times of sunset and sunrise respectively. The onset of flight during evening commenced *after* sunset from mid-September to mid-April, *before* sunset during the rest of the year. Onset of activity occurred at higher light intensities compared to light intensities prevailing during the return flight to the roost in the morning. The duration of activity time showed a curvilinear relationship with the duration of the night. The phase relationship between onset and end of activity, and sunset and sunrise, showed marked seasonal variations in the values of Ψ_{onset}, Ψ_{end}, and $\Psi_{midpoint}$. However, such changes in the phase angle properties did not obey Aschoff's seasonal rule. Based upon the data obtained on the onset and end of activity patterns for five species of bats, including the data from this study, we report that *P. mimus* is the earliest to set out for foraging in the evening and among the last to return home in the morning. This might be due to dusk and dawn peaks in activity of the prey insects.

Key words: Onset of activity – End of activity – Phase angle difference – *Pipistrellus mimus*

It is well established that the light-dark cycle is the most powerful entraining agent or *zeitgeber* in synchronizing the activity-rest patterns of animals especially the higher vertebrates (Aschoff et al. 1982). The timings of sunset and sunrise and the onset and end of activity of the animals are used as reference points to compare and demonstrate seasonal changes in their phase relationship (Aschoff et al. 1972; Chandrashekaran et al. 1983). Accordingly, a few investigations, which mainly rely on field studies, have been made on seasonal trends in the temporal changes in the activity pattern of birds and mammals (Daan and Aschoff 1975; Kenagy 1976). Among mammals, bats are nocturnal and Griffin and Welsh (1937) were the first to report endogenous rhythms in bats, even before describing their unique system of echolocation (Pierce and Griffin 1938). Erkert (1982) has described the seasonal changes in timing of activity patterns of temperate bats with respect to light-dark cycles under both field and laboratory conditions.

The Indian pygmy bat *Pipistrellus mimus* is small (3.6±0.4 g), and is one of the common microchiropterans of tropical India, living in a variety of habitats such as rocks or in any kind of crevices, thatches, tree holes and so forth. In this paper, we describe our observations on the activity/rest pattern of a small colony of *P. mimus* under natural conditions, and compare it with other species of bats. We demonstrate that among bats in our study area *P. mimus* is the earliest to leave and latest to return to its daytime roost over the seasons.

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Materials and methods

A colony of about 20 individuals of the Indian pygmy bat *P. mimus* occupied an unused tunnel which forms the southern and western sides of the building of the Department of Animal Behaviour and Physiology situated in the Madurai Kamaraj University campus (9°58′N, 78°10′E). The tunnel is 24 m in length, 0.85 m in width and 1.3 m in height and has an entry only through the western side. The bats roosted in groups, (mostly females) and singly (mostly adult males) inside the various crevices available in the southern part of the tunnel.

We conducted this study from May 1990 to August 1991. Visual observations on the timing of the outflying and homeflying activity at the entrance of the tunnel were made at weekly intervals. We considered the time at which the first bat left the tunnel during the dusk period as the time of onset of activity of the colony only if an another individual followed the first within 5 min. Similarly the time at which the last bat flew back into the tunnel during the dawn hours was considered as the end of activity of the colony. The time interval between the onset and end of activity was arbitrarily considered as the duration of activity of the colony (Erkert 1978; Marimuthu 1984; Usman et al. 1990). A correlation between the duration of night and the activity time was made by using polynomial regression: $Y = a + b_1x + b_2x^2 + b_3x^3$. The values of light intensity were measured during dusk and dawn by a UDT optometer.

The timings of sunset and sunrise were obtained from the table published by the Meteorological Department, Government of India, and were adjusted for the latitude of our study area in Indian Standard Time. The phase angle differences (Ψ) for onset, end and midpoint of activity of the colony were calculated by the following method (Daan and Aschoff 1975; Kenagy 1976):

Ψ_{onset} (Ψ_o) = time interval between sunset and onset of activity
Ψ_{end} (Ψ_e) = time interval between sunrise and end of activity
$\Psi_{midpoint}$ (Ψ_m) = 1/2 ($\Psi_{onset} + \Psi_{end}$)

Results

Light-sampling behaviour

Prior to setting out for foraging, the bats flew out around sunset and made circling flights repeatedly flying into and out of the tunnel. This light-sampling behaviour was observed at relatively high light intensities of 662 lux (± 795 SD; $n = 63$) and lasted 14 min (± 11 SD; $n = 65$) over the seasons. This pre-emergence activity was more intense on days with cloudy and drizzly weather.

Onset and end of activity

The onset of activity occurred *before* sunset from mid-April to mid-September (except on 6 August 1990; 7 and 28 June and 24 July 1991) and *after* sunset during the rest of the year (Fig. 1). At first the bats flew out singly, and after a few minutes groups of three to six individuals emerged. The time taken for the outflying activity of the colony, i.e. the time between the first and the last outflier, was 15 min (± 6 SD; $n = 62$) over the seasons. The average light intensity when the first bat flew out of the tunnel was 160 lux (± 176 SD; $n = 62$).

The homeflying activity pattern began during the predawn hours, and the last bat always returned before sunrise (Fig. 1) except on two cloudy days during August 1991 when the last bat flew back to the tunnel 5 min after sunrise. The termination of activity in the predawn hours always occurred at lower light intensities. Thus the light intensity at the time when the last bat flew back to the tunnel was 43 lux (± 52 SD; $n = 48$).

The duration of activity of the colony showed a curvilinear relationship with the duration of night (Fig. 2). A polynomial regression gives a good fit ($r^2 = 0.76$). From the ANOVA we find $F = 41.1246$, $df = 3{,}39$, $P = 0.0000$. The duration of night varied by 1.16 h over the seasons (11.30–12.46 h) and the activity period consequently varied by 1.00 h (11.08–12.08 h).

Phase angle difference

It was clear that the onset and end of activity of the colony changed systematically and showed a precise rela-

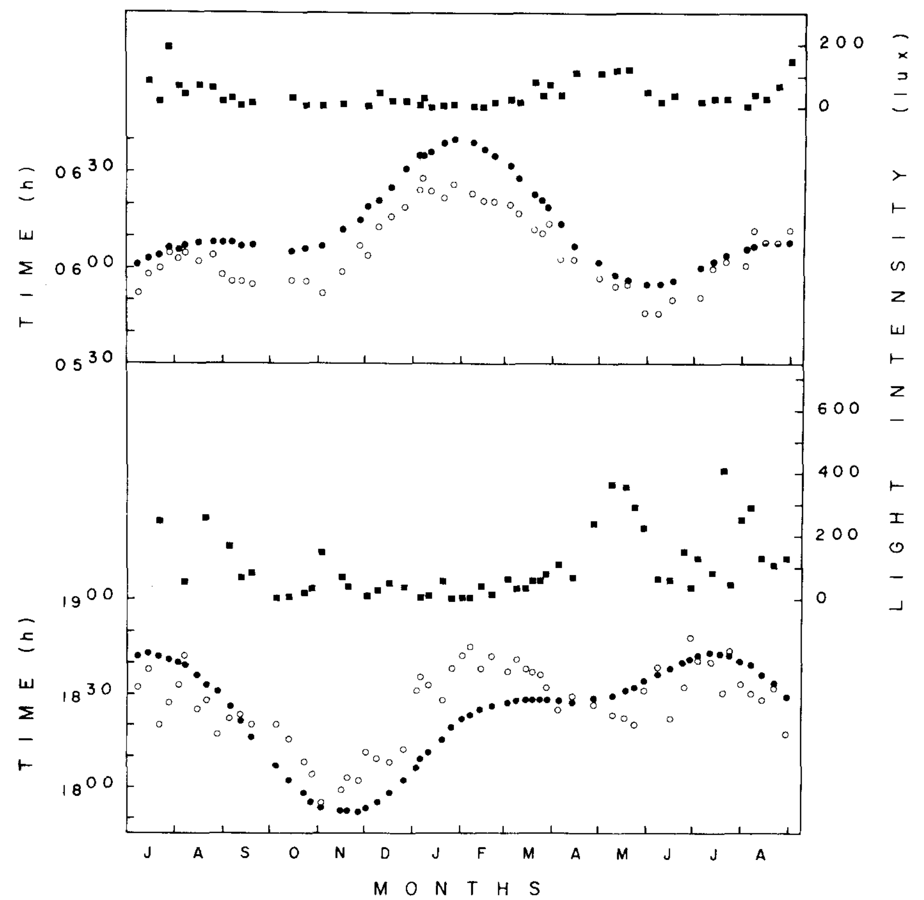

Fig. 1. The relationship between the times of onset and end of activity (*open circles* in the *lower* and *upper panels*, respectively) and time of sunset and sunrise (solid *circles* in the *lower* and *upper panels* respectively) over the seasons. The *solid squares* in the *lower* and *upper panels* indicate the values of light intensity over the seasons at the time of onset and end of activity, respectively

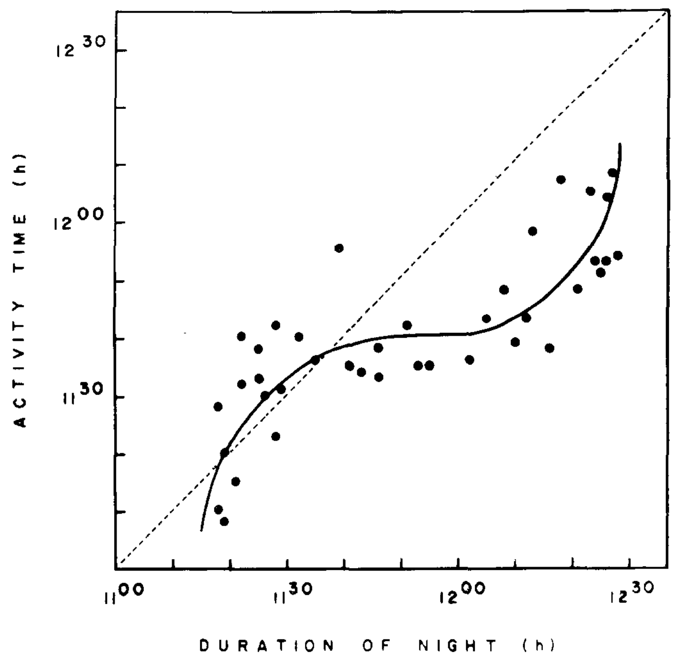

Fig. 2. The relationship between the duration of night and activity of the colony during the period of study. The *dotted line* shows the constant proportion. The *fitted curve* is given, by duration of activity time $= -3313.31 + 840.1 *$ (duration of night) $- 70.75 *$ (duration of night)$^2 + 1.98 *$ (duration of night)^3

tionship with the timings of sunset and sunrise respectively. The timings of sunset over the seasons varied by 51 min (17-52–18-43 hours) and accordingly the onset of activity displayed a range of 54 min (17-54–18-48 hours). Similarly, the timings of sunrise varied by 45 min over the seasons (05-55–06-40 hours) and the end of activity by 42 min (between 05-46–06-28 hours).

In Fig. 3, we present data on the phase-angle properties of the bat colony, with the largest Ψ_0 values (more positive) and smallest Ψ_e values (less positive) seen from mid-April to the end of August and the reverse from September to early April. As a result, the Ψ_o and Ψ_e values mirror each other. The seasonal trend of the phase angle for midpoint of activity (Ψ_m) showed less variation than Ψ_o and Ψ_e. The decrease in photoperiod during winter months resulted in more negative or less positive values of Ψ_m.

Discussion

The repetitive circling flights made around the entrance of the tunnel during dusk hours help the bats to assess the light intensity and the best time to leave for foraging. The light-sampling behaviour (Twente 1955; DeCoursey and Menon 1991) occurred a few minutes earlier on cloudy evenings and under such conditions the bats flew in and out of the tunnel more frequently. Interestingly, in a few observations the bats returned to the tunnel after travelling a distance of about 200 m when the light intensity increased due to the sudden dispersal of cloud cover. This shows that the light intensity plays an important role on the initiation and regulation of activity.

The onset of the outflying activity of *P. mimus* occurred in a greater range of environmental light intensity which, implies the absence of a threshold value for triggering the outflight. This is in contrast with earlier reports (Voûte et al. 1974; Erkert 1978) mentioning the occurrence of the emergence of bats at set and particular light intensities. The seasonal changes in the timing of

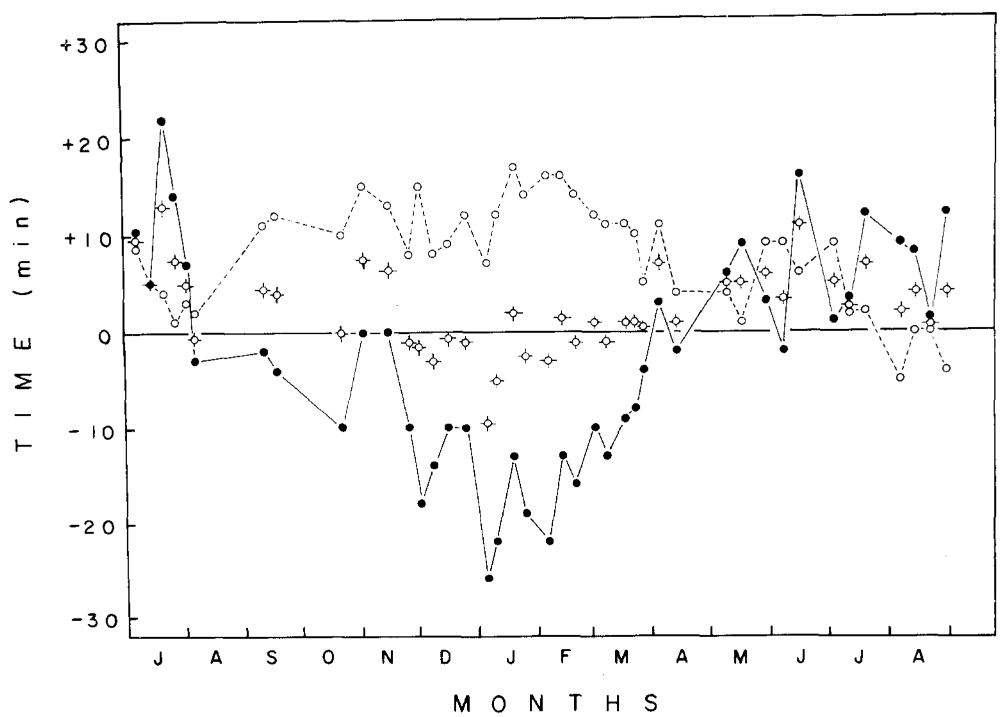

Fig. 3. Seasonal changes in the phase angle differences for Ψ_{onset} *(closed circles)*, Ψ_{end} *(open circles)* and $\Psi_{midpoint}$ *(unconnected circles)* over the seasons

Table 1. Timing of emergence of the first bat and return of the last bat and light intensity values for different bat species studied over the seasons in the same area

Bat species	Emergence (h)	light intensity at emergence (lux)	Return (h)	Light intensity at return (lux)	Reference
Megaderma lyra (36.3 g)	18.05–18.58	1–21	5.41–6.18	<19	Balasingh 1990
Taphozous melanopogon (20.0 g)	18.25–18.41	0.1–50	[a]	[a]	Subbaraj 1979
Rhinopoma hardwickei (13.5 g)	18.05–18.53	1–60	5.33–6.20	<10	Usman et al. 1990
Hipposideros speoris (13.0 g)	18.05–18.45	4.5–40	5.37–6.20	<45	Marimuthu 1984
Pipistrellus mimus (3.6 g)	17.54–18.48	0.64–689	5.46–6.28	<194	Present study

The mean values of the body weight are given in parentheses
[a] Data not available

activity onset also indicate continuously changing and compensatory processes with regard to triggering light intensities. Thus *P. mimus* may be seen to fly out in virtual sunlight on summer evenings and in darkness on winter evenings. The end of activity occurred at considerably lower illumination possibly to avoid predation by birds of prey, which begin their foraging activity before sunrise (Erkert 1982).

The seasonal changes in the timings of onset and end of activity reflect the change in the duration of activity (α) over the seasons. As reported for other mammals (Kenagy 1976; Erkert 1978; Georgii 1981; Marimuthu 1984) in *P. mimus* we found a correlation between α and duration of night and obtained a reverse S-shaped curve. There are limits to the parallel changes between the duration of activity and night length. Even bats living in tropical and subtropical areas (Zack et al. 1979) far from the equator and bats living in subarctic regions (Swift 1980) are not able to extend or curtail their activity to parallel the length of the night.

In consonance with the theory of oscillation (Aschoff 1969) more negative Ψ_{onset} and more positive Ψ_{end} values are obtained during winter months for our bat, as reported for other night-active animals including bats (Kenagy 1976; Pohl and West 1976; Marimuthu 1984; Usman et al. 1990; Balasingh 1990). However, the seasonal changes in $\Psi_{midpoint}$ values do not obey the 'seasonal rule' (Aschoff 1964), which states that the summer increase in photoperiod should result in an increased (more positive) $\Psi_{midpoint}$ in day-active animals and decreased (less positive or more negative) $\Psi_{midpoint}$ in night-active animals. In fact, $\Psi_{midpoint}$ details for *P. mimus* have many features in common with $\Psi_{midpoint}$ trends postulated for day-active species by Aschoff's seasonal rule. Studies on four other microchiropteran bats, *Taphozous melanopogon* (Subbaraj 1979), *Rhinopoma hardwickei* (Usman et al. 1990), *Hipposideros speoris* (Marimuthu 1984) and *Megaderma lyra* (Balasingh 1990), in the same area showed that their activity pattern obeyed the seasonal rule. Studies on the circadian organisation of flight activity of *P. mimus* under laboratory conditions may reveal more details on its phase relationship with light – dark cycles and with other species of bats.

The activity/rest pattern of *P. mimus* seen in this study is apparently unique. *P. mimus* also happens to be the earliest to set out for foraging in the evening and latest to return to the roost compared to the other species of bats living in the same study area (Table 1). This may be due to the occurrence of dawn and dusk peaks of the activity of mosquitoes (Pandian and Chandrashekaran 1980) which form the major food item of *P. mimus* (Khajuria 1980). The activity of the Japanese house-dwelling bat *P. abramus* was also synchronized with the emergence of its prey insects (Funakoshi and Uchida 1978). Speakman (1990) reported that daylight flight activity of pipistrellid bats coincided with high insect availability and opined that its primary function was feeding. However, the early outfliers like *P. mimus* are more vulnerable to predation. We observed that the black-winged kite *(Elanus caeruleus)* caught some *P. mimus* ($n = 6$) individuals while they were flying out of the tunnel.

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